

XXIV. *On the Respiration of Insects.* By GEORGE NEWPORT, Esq. Member of the Royal College of Surgeons, and of the Entomological Society of London. Communicated by P. M. ROGET, M.D. Sec. R.S.

Received and Read June 16, 1836.

*Respiration.*

IT has been long proved by many physiologists that insects produce the same changes in the atmosphere during respiration as other animals. REAUMUR, BONNET, SCHEELE, HUBER, EDWARDS, AUDOUIN, and others, have all shown that the results of the respiration of atmospheric air by insects are the production of carbonic acid gas, and the loss of oxygen; but these results vary in degree in different genera,—in the different states of the same insects,—and at different periods of the year. My object, therefore, in this paper will be to show the relative quantity of air consumed by different tribes of insects in their different states,—the power which particular insects have of supporting existence in different media,—and the relation which this power and the consumption of air bear to the comparative volume of the structures concerned.

The life of an insect has been considered by naturalists to have three distinct periods, the larva, the pupa, and the perfect state; but each of these periods, in so far as the functions of the different structures of the body are concerned, although tending only to the production of the perfect individual, is in itself a distinct condition. Thus the respiration, circulation, temperature, food, and locality of the insect are in general all different in the different states. In the earliest period of the larva state the respiration is much feebler than when the animal has nearly arrived at its full size, and the circulation of its blood is much quicker; but the relative quantity of its food is much greater, in proportion to its bulk, in the latter than at the earlier period, and its power of generating heat increases as it approaches to its adult condition. In the pupa state also there is a change in all these functions. In many genera the insect ceases to eat; its circulation becomes slower than at any other period; its respiration is greatly diminished in frequency and volume; and its power of generating and of maintaining a temperature of body above that of the surrounding medium, which every individual insect constantly preserves when in a state of activity, is now almost suspended. In the perfect, or imago, state there are other changes in these functions. The respiration again increases in frequency and volume; the power of generating and of maintaining heat is very much augmented; the circulation is more rapid than at any other period, while the necessity for a constant supply of food is often less

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urgent than in the larva state. Hence it is evident that much caution is necessary in drawing conclusions from our observations on the function of respiration in insects in their different states, and that where quantity of air is concerned the relative volume of the organs of respiration must not be forgotten.

*Parts concerned in Respiration.*

The parts more immediately concerned in respiration are the tracheæ and spiracles, the first of which undergo very great changes during the transformations of the insect. The next are the muscles and the nerves distributed to them.

1. *The Tracheæ.*

*The tracheal vessels* in the larva of *Sphinx ligustri*, L., consist, as described by LYONET and others in the *Cossus ligniperda*, of a series of tubes conveying air like the bronchial tubes and tracheæ of other animals; but instead of being composed of only one set communicating with the mouth, as in vertebrated animals, they are multiplied in number, and are arranged along each side of the body of the insect near the middle line, between the dorsal and ventral layers of longitudinal muscles. There are nine sets of tracheal tubes on each side, corresponding to the nine outlets or spiracles. The first is situated in the second segment, behind the head, and the remaining eight are in the fifth and succeeding segments to the last or anal one. The different sets are connected together by two longitudinal tracheæ, one on each side of the body, and communicate by very short tubes from these tracheæ with the spiracles.

*The structure* of the tracheal tubes has been described by SWAMMERDAM, SPRENGEL, and others. The tracheæ are formed, as described by SPRENGEL, of two membranes, an external serous, and an internal mucous, inclosing between them a spirally convoluted elastic fibre [Plate XXXVI. fig. 1. *a.*], which gives them the appearance of the tracheæ of other animals. The external or serous membrane [*b*] is very loosely attached around the middle or spiral structure. The whole mucous or internal lining is continuous with the cuticle or external covering of the body, and is thrown off and renewed whenever the insect changes its skin, as noticed by SWAMMERDAM, DEGEER, LYONET, and BONNET; although SPRENGEL seems to consider this as not a true membrane, but as only forming a means of connexion between the coils of the middle or spiral fibre. I have seen this lining membrane of the tracheæ thrown off with the skin of the larva at every period of its change in almost every order of insects, but more particularly in the genera *Apis*, *Papilio*, and *Scarabæus*, and am satisfied that it is a distinct structure, and is not merely that portion of the membrane which lines the entrance of the tubes which is thus thrown off, but the complete lining membrane of the ramified tracheæ.

Each set of vessels consists of from eight to ten or twelve tubes, which originate in a bundle from the longitudinal tracheæ, and distribute their branches over the stomach and other viscera, sending minute anastomosing ramifications to every part

of the body, even into the substance of the brain and nerves. The longitudinal tracheæ communicate freely with each other across the body, both at the anterior and posterior part of the insect, and along the whole dorsal and ventral surfaces, by small ramifications of the tracheæ from each side meeting and anastomosing together. At the anterior part of the body there is also a large tracheal tube communicating between the tracheæ of the sides. It is situated in the second segment, and extends into the base of the first, where it gives off, immediately behind the brain, four principal branches, which are distributed forwards over the brain and head. Two of these go to the antennæ, and the others to the anterior and upper part of the head. There is also a large branch from the under surface of the longitudinal trachea in the second segment, which communicates across the under surface of the segment with a corresponding one from the opposite side. This is the general arrangement of the tracheæ, particularly in the larva state of insects. The larva of the Bee has the tracheal vessels very small, but freely communicating around the body, as was shown by SWAMMERDAM. The same insect in its perfect state has these communications still existing, but the whole of the principal tracheæ are then developed into large vesicles or bags. This is the case even with those tracheæ which traverse the under surface of the abdomen, although the tubes of communication are not obliterated [Plate XXXVI. fig. 2. g.]. All volant insects in their perfect state have the respiratory organs of the same vesicular structure.

*The vesicles*, as was shown by SWAMMERDAM \* and SPRENGEL, are covered with innumerable punctured spots, which are only perceptible under a good microscope, and when attentively examined exhibit somewhat the appearance of perforations. MARCEL DE SERRES and STRAUS DURCKHEIM deny the existence of spiral fibre in these vesicles, but SUCKOW and BURMEISTER † are of opinion that it really does exist, and I am myself disposed to maintain the same view. Indeed when we remember that the vesicles exist only in the perfect insect, and are only dilated tracheæ, and that in tracheæ the existence of spiral fibre is undoubted, it surely cannot be questioned that it exists also in the vesicles, although probably in a very attenuated state, and almost atrophied. The nature of the punctured spots in the vesicles is of some interest, since I am not aware that they have been distinctly observed until after the insect has passed into the perfect state. BURMEISTER, who contends for the existence of spiral fibre in the vesicles, conceives that these spots are occasioned by the rupture of the spiral fibre during development, and are formed by the interspaces between the portions of ruptured fibre. That this cannot be the case is proved by the existence of these spots in some of the tracheæ which communicate directly with vesicles, and have not been dilated, in which the spiral fibre is distinctly seen to be unbroken; and also by the circumstance of their not being in a regular series, or in the course of the fibres in the vesicles, but distributed thickly and irregularly over the surface of the whole vesicle, and by their existing between two parallel fibres, and even in the

\* Biblia Naturæ, Plate XXIX. f. 10.

† Manual of Entomology, translated by SHUCKARD, 1836, p. 181.

substance of fibres, as I have distinctly seen them in the vesicles of the male Humblebee, *Bombus terrestris*, STEPH. Besides this, I have also observed them terminating in an abrupt and remarkable manner in the dilatation of the large tracheæ in the same insect; and I have also seen them in some of the larger tracheæ themselves, as was observed and figured by SWAMMERDAM in *Oryctes nasicornis*, STEPH. The existence of these punctured spots so universally in perfect volant insects, leads us to inquire into their probable use. After many careful examinations I am disposed to believe that these spots are only partial perforations of the vesicular structures,—that they do not pass through the internal or mucous lining,—and perhaps are little cells or receptacles in the coats of the vesicles, in which the circulatory fluid can be most freely submitted to the action of the air in the vesicles through the delicate mucous lining, as in the minute terminal air-cells in the respiratory organs of vertebrated animals.

When the tracheal vessels have become developed into pulmonary sacs, those of each segment may be considered as analogous to, and as only a repetition of, the tracheal structures in Vertebrata. A very large proportion of the ramifications from each centre or spiracle in the larva of the Sphinx and other Lepidoptera is distributed over the alimentary canal. Those which are given to the œsophagus and stomach extend from the second to the tenth segment, while those which go to the duodenum are from the eleventh, and those to the colon and cæcum from the twelfth and thirteenth. The minute branches of these vessels pass between the fibres of the muscular coat of the alimentary canal, and are distributed upon the mucous coat, between it and a structure which I believe has not hitherto been described, the *adipose coat*, which lies between the mucous and muscular coats, and into which the ultimate ramifications of the tracheæ are extended. This layer is very distinct in the alimentary canal of *Cerura vinula*, STEPH., particularly in the colon and cæcum [Plate XXXVI. fig. 3. a. b.]. All the secretory and generative organs are furnished with minute anastomosing branches in abundance, even the dorsal vessel itself, and the ovarial tubes. They are distributed through the limbs, even to the extremities of the tarsi in the perfect insect, and through the antennæ and eyes.

*The development* of the air-vessels into sacs or bags in volant insects begins to take place a little before the insect changes into the pupa state. In all larvæ which undergo a complete metamorphosis, when passing into the pupa state, the respiratory organs are distinctly tracheal, without any dilatations; and this is more strictly the case in those insects which afterwards have the largest vesicles, as in the *Scarabæi*, *Lucani*, *Lepidoptera*, and *Hymenoptera*. In lepidopterous insects the tracheæ do not appear to undergo any marked change until about the time when the insect has ceased feeding. Those which are the first dilated in the Sphinx are from the second and fifth spiracles. These, with the anterior portions of the longitudinal tracheæ, become a little dilated soon after the insect has entered the earth, and is forming the cell in which it is to undergo its transformation. In the Butterfly (*Vanessa urticae*, STEPH.), which does not enter

the earth but suspends itself in the open air, the change begins to take place while the insect is spinning its thread for this purpose. When it has remained a few hours at rest, preparatory to undergoing its transformation, the tracheæ become enlarged; and at about the period when the change to the pupa state takes place the insect appears to make several powerful respiratory efforts, accompanied with much muscular exertion, and these are continued at intervals until its old skin becomes fissured, and is gradually thrown off. The tracheal vessels of the fifth and sixth segments, at this period of changing to the pupa state, begin to assume the vesicular form, and become more and more dilated during the first few days after the change. In the Sphinx, and those insects which pass the winter in the pupa state, there appears to be an interval, or cessation in the development of the tracheæ, as well as of all the other structures, during hybernation; but when the changes have again taken place in the spring the development continues until the respiratory organs occupy a very large proportion of the body of the insect; so that when the insect has arrived at the perfect state, the longitudinal tracheæ in the thorax are exceedingly large canals, leading to, and communicating with, the roots of the wings in the thorax and the air-bags in the abdomen. There are four of these air-bags on each side of the abdomen in the Sphinx and other Lepidoptera. The largest are close to the posterior part of the trunk or thorax, the others gradually decrease in size as they approach the anus. In the male Humble-bee, *Bombus terrestris*, STEPH., the anterior vesicles are exceedingly large, and form, with those which follow them, a series of very freely communicating respiratory cavities, while a nearly similarly free communication exists between the two sides of the body in the transverse tracheæ, which are dilated into a series of funnels which communicate with each other across the body by their apices [Plate XXXVI. fig. 2. g.].

In those insects which undergo their changes in the open air without entering the earth, and which pass but a few days in that condition, there is no interval or period of suspension of development. In the common Nettle Butterfly, *Vanessa urticae*, which during the summer undergoes its changes in at most fourteen days, and very often, if the season be favourable, in eight or nine, the changes in the respiratory organs have distinctly begun to take place about *two hours* after the insect has suspended itself for transformation. MECKEL has observed that the air-sacs are found in the insect soon after it has entered the pupa state; but I have found that the dilatation of the tracheæ, which are developed into these sacs, commences very much earlier. On examining the insect about *half an hour* before it changes to a pupa, I have always found the whole of the tracheæ a little distended, particularly those in the under surface of the thorax, from the first two pairs of spiracles, but their distribution to the stomach and intestines has continued as regular as in the active larva. It is at the actual moment of transformation that all the changes take place most rapidly. The efforts which the insect makes at that time appear very much to affect the condition of the respiratory organs. When the insect has fissured and thrown

off its old skin as a larva, there is a cessation of its efforts for a few seconds. It then makes a few slow but very powerful respirations, during which, as in every forced inspiration, the abdominal segments are much distended, after which the longitudinal layers of muscles of these segments become very much contracted, and the segments themselves shortened. While this is taking place the circulatory fluid contained in the vessels of the abdomen is propelled forwards, and the wings, which at the moment of slipping off the old skin are scarcely so large as hemp-seeds, are distended at their base, and at each inspiration of the insect are gradually enlarged by the propulsion of circulatory fluid into them, and are carried down over the lateral and under surface of the trunk, and the ventral surface of the first two segments of the abdomen. This is exactly what takes place in the *Sphinx ligustri*, as well as in *Vanessa urticae*. From the fact of all the tracheæ being enlarged immediately after the insect has changed to the pupa state, it seems not improbable that this enlargement is occasioned by the closing of the spiracles, and the expansion of the air within the tracheæ during the powerful respiratory efforts of the insect in effecting its transformation,—that it results from the recession of the circulatory fluid from the vessels of the abdomen into the partially developed wings taking off pressure at the instant from the tracheal tubes, which then become distended by the natural elasticity of the air contained within them.

Professor CARUS attributes the development of the air-bags and dilatation of the tracheæ entirely to the closing of the spiracles and the expansion of the contained air, which he thinks is *increased in quantity*\* during the development of the insect. But it seems more probable that the formation of air-bags is occasioned simply by a continuance of the same cause, the elasticity of the contained air, which produces the enlargement of the tracheæ in the first instance, and that this enlargement or dilatation keeps pace with the gradually decreasing size of the digestive organs, since the spiracles are not permanently closed during the pupa state, but are in constant action, except during the period of complete hybernation. It is at the actual moment of transformation that the anterior pair of large vesicles begins to be formed, and the tracheæ in the next segment are a little more enlarged. The antennæ, which just before the change were coiled up within the sides of the head, are now extended along the sides and abdomen, and the tracheal vessels within them may be readily examined. If the antenna be separated from the pupa while soft and transparent, it will be seen that the trachea within it extends from its base to its apex [Plate XXXVI. fig. 5. a. b.]. It is a continuation of a large trachea that comes from the first spiracle, and crossing the segment above the œsophagus and dorsal vessel, sends off its cruciform branches immediately behind the brain, at the back part of the head. There are four branches given off at that point, as before noticed; the two external ones are those which supply the antennæ. The main tracheal vessel of the antenna at this period of the insect is very small, but afterwards becomes much enlarged.

\* Introduction to Comparative Anatomy, translated by GORE, 1827, vol. ii. p. 167.

It passes along the antenna nearest its under surface, and in the *Vanessa urticae*, STEPH., gives off laterally thirty-four pairs of minute branches, one pair to each segment.

In the twelve segments which constitute the club or apex of the antenna, the trachea becomes very minute, and in the last four segments of the club it is divided into numerous ramifications [Plate XXXVI. fig. 6. *b.*]. About *an hour* after the change to the pupa state the tracheæ from the first spiracle, which ramified over the œsophagus, are enlarged to about double their original size, and instead of continuing of a pencillated structure, are almost of equal diameter throughout, and are beginning to be detached from the œsophagus, which is becoming narrower. At *seven hours* these changes have all been carried further, and the air-cells in the abdomen are much larger. At *twelve hours*, besides the gradual enlargement of the tubes, the chief thing observable is the diagonal direction of the tracheæ from the seventh spiracles, which supply the pyloric extremity of the stomach, which proves that the stomach is gradually becoming shorter previous to the detachment of these tracheæ, which subsequently takes place. *Eighteen hours* after the change all the longitudinal and thoracic tracheæ, with those of the head, are still further enlarged, and the tracheæ from the third pair of spiracles, which are given to the cardiac extremity of the stomach, are partly detached from that organ, and are more dilated than any of the others. The tracheæ from the ninth spiracles, which are given to the colon, are beginning also to assume a vesicular form. The stomach is still supplied with tracheæ from six spiracles. At *twenty-four hours* the changes are still advancing. At *thirty-six hours* the tracheal branches distributed to the different ganglia are enlarged; and at *forty-eight hours* the development of these parts is so far advanced that nearly all the tracheæ in the body have become a little dilated, and this dilatation continues until the insect has become perfect. The only difference between the development of this insect and the Sphinx, or those which undergo their metamorphoses in the earth and remain in the pupa state during the winter, is in the rapidity of the changes; and even this difference exists only in those diurnal insects which are developed in the beginning and middle part of the summer, since in those individuals which are produced late in the season, and consequently remain in pupa through the winter, all the circumstances are precisely similar. The real use of the pulmonary sacs, which are found in all volant insects, appears to be, as supposed by JOHN HUNTER, to enable the individual to alter its specific gravity at pleasure by enlarging its bulk, and thus render it better able to sustain itself on the wing with but little muscular effort. That this is the real use of the sacs may further be inferred from their non-existence in the larva or infant condition of the insect, and from their almost entire absence in all insects which are destined to live entirely on the ground. This opinion is further supported by the fact that they are most developed, relatively to the size of the individual, in those insects which sustain the longest and most powerful flight, as Hymenoptera, Lepidoptera, some of the winged Coleoptera, the Hemiptera and Lucani, while in none of these insects in the larva state is there any-

thing approaching to sacs, but the respiratory organs are purely tracheal. The common Humble-bee, which has the largest pulmonary vesicles of any insect in the perfect state, has its respiratory organs in the larva state exceedingly small and pencillated. But further proof of the vesicles being for the sole purpose of lightening the body is to be found in the male *Lucanus cervus*, LINN. In that insect the large and apparently heavy mandibles and head, instead of being filled with solid muscles, are filled almost entirely with a string of vesicles, which are developed from the sides of some large tracheæ that extend through the mandibles. By this beautiful provision of nature these apparently heavy and unwieldy structures are rendered extremely light, while their solid exterior fits them for all the purposes of strength and defence required by the insect.

## 2. *The Spiracles.*

The *structure* of the spiracles, the orifices of respiration, is somewhat complicated. In the larva of *Sphinx ligustri*, L., the spiracles are oval apertures closed externally by valves, which open perpendicularly in their long axis, like the iris in feline Mammalia. They are placed on a level with the external or cuticular surface of the body, and are formed by a series of converging fibres, edged, as in the iris, by circular ones [Plate XXXVI. fig. 6.], and guard the entrance of the spiracles. At a little distance within this valve the spiracle is considerably enlarged, and there is situated a second valve, of a more complicated structure. The anterior half of this second valve [Plate XXXVI. fig. 7. *a.*] is of a darker colour and firmer substance than the outer valve. Its inner surface, or that which looks towards the viscera, is concave, and its margin crescent-shaped, and it is not acted on by any muscles. The posterior portion of the valve [fig. 7. *b.*] is thick, moveable, and of a dark colour, and closes on the anterior half like a cushion or pad. This portion is acted on by a remarkable muscle, the *retractor valvulæ* [fig. 7. *c.*], composed of five distinct fasciculi of fibres uniting in a common tendon, and by their conjoined action opening the valve, just as the *levator palpebræ* elevates the eyelid in Man and other animals. The tendon into which the converging fasciculi of this muscle are inserted, passes diagonally upwards and backwards, and is inserted into a little elevation in the common tegument of the body. A few circular fibres surround the edges of the inner valve [fig. 7. *d.*] of the spiracle, and constitute the sphincter muscle which closes the valve. It is among these fibres that the retractor muscle originates. The sphincter muscle and valve are still further acted upon by another muscle, which may be considered the great constrictor muscle of the spiracle, *retractor spiraculi* [fig. 7. *e.*]. This muscle originates from the *posterior margin of insertion* at the anterior ventral surface of each segment, at a little distance from the median line [Plate XXXVII. fig. 26.], and passing diagonally upwards and outwards terminates in a tendon, with which some of the fibres of the orbicular muscle are blended. The internal or proper valve of the spiracle appears to be continuous with the mucous lining of the tracheæ



[Plate XXXVI. fig. 7. *a. b.*]. CARUS has noticed a similar structure in the *Grylli*, but has not described it further than as resembling an eyelid\*. He seems to have thought it simply a reduplication of the mucous membrane, but has taken no notice whatever of the muscles belonging to it.

*The Muscles concerned in Respiration.*

The muscles concerned in the function of respiration, besides those which properly belong to the spiracles, include those of each entire segment of the body. Every act of *inspiration* is of a mixed character, and is partly a voluntary effort of the animal, and partly dependent upon those combined laws of the animal economy which, depending upon each other for their continuance, constitute organic life. These laws have justly been designated the involuntary functions of the body. Every act of *expiration*, in the natural state of the animal, is more of an involuntary than of a voluntary character, and may be regarded simply as a disposition in the muscles concerned to regain their previous condition, which is intermediate between contraction and relaxation, and takes place independently of the will of the animal.

As every act of respiration thus consists of two distinct efforts, it necessarily requires the consentaneous action of all the muscles of the parietes of the abdomen and trunk in vertebrated, and of all the muscles of a segment of the body in invertebrated animals. This is really what takes place in respiration. In Man all the muscles of the chest and abdomen are in constant action; so are all the muscles of the segments in insects, whether the animal be awake or sleeping.

The muscles of a segment of the body in the larva of *Cossus ligniperda* have been minutely described by LYONET, but as I shall presently have occasion to notice the particular nerves which are distributed to them in the *Sphinx ligustri*, I must be permitted to describe those of the ventral surface of a segment in the larva of that insect

Those muscles which form distinct layers or sets, and act together, are generally inserted into slightly elevated ridges in the skin, while a single muscle, or the tendon of many muscles united together, is attached to a tuberculated elevation. The skin is there thicker than in other places, and thus affords a means of attachment. There are always three ridges for the insertion of muscles between two abdominal segments. The middle one is the largest, and affords both origin and insertion to the straight or longitudinal muscles, while the others in like manner afford origin and insertion to the oblique ones.

On removing the fat and viscera from the abdomen of the larva, the first layer which presents itself, and forms the interior parietes of the body, consists of many longitudinal fibres, like the *recti abdominales* of vertebrated animals. These muscles extend from the anterior part of the under surface of the second segment to the posterior part of the eleventh and twelfth; but it is only at the commencement of the

\* CARUS, Comparative Anatomy, by GORE, 1827, vol. ii. p. 162.

sixth, which is in reality the commencement of the true abdomen, that they can properly be considered as recti muscles, since it is at this part where they begin to be most developed. While passing through the thoracic region they are thinner, narrower, and somewhat differently arranged. They are the most powerful of all the muscles of the abdomen, and are those which are most concerned in contracting and effecting the duplicature of the external teguments during the changes of the insect, and mainly assist in locomotion during the larva state. There are four sets of these muscles in the abdomen [Plate XXXVII. figg. 1. 1.], two on the dorsal and two on the ventral surface on each side of the nervous column and dorsal vessel. These muscles on the ventral surface are again divided into four sets, two on each side of the nervous column [figg. 1, 2.], and between which there is a slight interspace. The set which is situated on each side nearest the nervous column consists only of three narrow fasciculi of fibres, and may thence be called *recti minores* [fig. 2.]; while the other set, situated more externally in the segment, is broad and powerful, and consists of from twenty to twenty-five distinct fasciculi, and may thence be named *recti majores* [fig. 1.]. The attachments of these are different from those of the smaller recti. The larger recti are inserted into the middle ridge of attachment, which forms the margin of each segment [figg. 3, 3.], close to the insertion of the muscles of the preceding segment; while the smaller are inserted at about one fifth of a segment further back [fig. 4.] towards the tail, or extremity of the body, and pass over the ridge of attachment for the larger recti to their insertion in a corresponding part of the next segment. There is a small muscle which originates from the same line of attachment as the greater rectus, between it and the smaller, which goes to the stomach and attaches that viscus to the exterior tegument of the body, and may thence be called *retractor ventriculi* [fig. 5.]. There is one of these on each side the nervous column, from the fourth to the eleventh segment. On removing the recti we expose two layers of very thin fine muscles. The upper layer consists of nine distinct fasciculi of fibres, which pass backwards and outwards in a slightly diagonal direction [fig. 6.], but less so than those of the second layer [fig. 7.], which lies immediately beneath it. This consists of seven distinct fasciculi, which originate from the anterior margin of the segment close to the smaller recti and beneath the larger, and extend about half the breadth of the latter across the segment. They run backwards and outwards in a diagonal direction, and are attached below the recti as far as their outer margin [fig. 8.]. These layers of fibres, when in action, draw the outer anterior margin of the next segment towards the middle line of the body, and consequently when those of several segments on one side of the body act together they bring forwards the posterior portion of the body of the same side, and bend it in a semicircular direction. If these muscular layers on both sides of the body act together they draw forwards the posterior part of the body in a straight line. Immediately beneath these there is another diagonal layer of fibres, which originates close to the median line of the body [fig. 9.] beneath the nervous column, and a little anterior to the insertion of

the smaller rectus. The origin of this set is exceedingly narrow, and resembles the origin of the oblique abdominal muscles from the crest of the pubis in Man. It is distinctly tendinous, and does not extend quite so far as the outer margin of the smaller rectus. This layer of muscular fibres begins to expand immediately above its origin, and is inserted beneath the greater rectus throughout nearly the whole extent of that muscle across the segment [fig. 10.]. When these oblique fasciculi are employed alone, they are evidently opposed to the latter, and draw the posterior part of each segment backwards and to the median line of the body; consequently they bend the anterior part of the body into the segment of an arch, and when both are in action they bend the anterior part of the body backwards. These muscular layers, from their form and direction, may be called the *first* [fig. 6.], *second* [figg. 7, 8.], and *third* [figg. 9, 10.] oblique. Beneath these there is another set of oblique fibres, which is formed of only two broad fasciculi. It originates from the anterior of the three ridges of attachment a little towards the inner edge of the smaller rectus [fig. 2.], and passing a little diagonally forwards and outwards beneath the great oblique, is attached to the third ridge of insertion, and may be called the *fourth oblique* [fig. 11.]. Beneath the posterior extremity of this set lies the *third* rectus, which is formed by three muscular fasciculi [fig. 12.], rather broader than those which constitute the second or smaller rectus, but running in the same direction longitudinally, and having the same origin and insertion. On removing the third rectus we arrive at the eighth layer of muscular fibres. This arises from the anterior ridge of attachment, and is formed by three rather broad fasciculi, which are partially crossed at their origin by the third rectus. This layer passes diagonally outwards, and is inserted into the third ridge as far as the outer margin of the great rectus and third oblique, which cover it, and may be called the *fifth oblique* [fig. 13.]. When this layer is removed we have exposed the triangular and transverse muscles. The *triangularis* [fig. 14.] consists of nine distinct muscular fasciculi, originating in a longitudinal series very near the median line of the body, alongside the nervous columns, and extending through the posterior half of the segment. The posterior of these fasciculi originates by three, and the one immediately preceding it by two, distinct heads or tendons, which, with the tendons of the other fasciculi of this set, indigitate with a set of short transverse muscular fibres [fig. 15.], ten in number, which occupy the median line beneath the nervous columns, and may be called the *transversus medius*. The fibres which form the triangular set pass backwards and outwards, with varying degrees of obliquity, and are inserted by strong tendons into the anterior transverse margin, or ridge of insertion [fig. 16.]. When this layer acts with its fellow of the opposite side it shortens the posterior half of the under surface of the segment; but when it acts singly, or in conjunction with the great or third oblique, it shortens that side of the segment, and bends that part of the body to the opposite side. It is a very powerful muscle in locomotion, and is probably also of great use in contracting the segment during transformation. The *transversi abdominales* [fig. 17.] are short, and consist of

six rather broad and thick fibres, which form two sets, and originate at some distance from the median line, posteriorly to, and on the outer side of the tendons of the great oblique, and passing outwards are inserted into the integument about half way across the segment. They contract the under surface very powerfully, and bring the sides towards the median line. Anteriorly to these muscles, but further from the median line, is another set, the *abdominales anteriores* [fig. 18.], consisting of six short muscles, which are inserted into the inferior margin of the lateral surface of the body. The *abdominales laterales* arise in the posterior half of the segment by three great fasciculi of narrow tendons [fig. 19.], eight in the first, four in the second, and seven in the third. These tendons are formed from very powerful muscles, which interlace with each other, and are inserted at different distances of attachment posteriorly to the spiracle [fig. 20.]. These are the great muscles of the false feet, and are connected at their origin with other transverse muscles near the median line. When these muscles are removed there are two layers of fibres which arise from the anterior line of attachment in the posterior part of the segment. The inner layer, or *obliquus posterior* [fig. 21.], consists of nine small muscular fasciculi of fibres, which pass diagonally outwards, and are inserted into the skin at different distances beneath the lateral abdominal muscles. The other set consists also of nine distinct fasciculi [fig. 22.], which arise from the same margin in the lateral part of the segment, and after crossing over the last lateral abdominal, pass between it and the one immediately before, and are inserted into the integument: they may be called the *postero-laterales obliqui*. Besides these layers of muscular fibres there are four other sets which seem particularly concerned in the function of respiration. The first of these, the *transversus lateralis* [fig. 23.], arises tendinous from beneath the outer margin of the great ventral rectus, and passing upwards and outwards internal to the great longitudinal trachea, which it crosses, is gradually enlarged, and is inserted a little beneath the external margin of the dorsal rectus. The second *transversus lateralis* [fig. 24.] arises lower down than the first, and is inserted beneath the dorsal rectus at about half way across the segment. These muscular fasciculi appear to be directly concerned in contracting the segments in expiration. The other two muscles of respiration have been noticed when speaking of the spiracles. The first, *retractor spiraculi* [fig. 25.], as before noticed, originates from the third ridge of muscular insertion, at the anterior part of the segment, on the ventral surface, by a small tendon before the transverse abdominal muscles [fig. 26.]. It gradually increases in size, and passes upwards and obliquely outwards and backwards, and terminates in a tendon which is inserted, as before described, into the circular fibres which surround the spiracle. This muscle appears to be directly concerned in forcible expiration, during which it draws the spiracle inwards and downwards, and when the fibres which surround the spiracle and form the orbicular muscle act in conjunction with it, it assists in closing the spiracle. The other muscle directly concerned in the function of respiration, *retractor valvulæ*, is the immediate antagonist of the last, and has been described as one of the proper muscles of the spiracle [fig. 27.].

These are the muscles which more particularly claim our attention, in order that we may see what nerves are distributed to them, and consequently what nerves are most concerned in respiration.

*Nerves concerned in Respiration.*

The nerves concerned in respiration, like the muscles, include those of the whole segment. In a former paper I have particularly described those nerves which, from their distribution, were considered to be more especially concerned in respiration. My endeavour now is to trace these and the moto-sensitive nerves to their terminations in the different layers of ventral and lateral muscles.

The inverted position of the nervous cords in insects and other Invertebrata has not a little confounded the right understanding of the analogy which exists between the nervous cords of vertebrated and invertebrated animals, and has given an appearance of probability to the opinion entertained by some anatomists that the cords in Invertebrata are not analogous to the spinal cord of Vertebrata, but to the sympathetic system. Even some of those who now believe that these cords are really analogous to the cerebro-spinal system of the higher animals, can hardly reconcile this opinion with the fact of their being situated along the ventral instead of the dorsal surface of the body. The reason for this change of position of the cords in Invertebrata appears to be partly to protect the cords themselves, and partly that the nerves may be supplied to the limbs without having to travel round the sides of the body, and thereby be exposed to the hazard of injury, which they would be were they situated along the dorsal surface as in Vertebrata. But notwithstanding this change of position of the cords in Invertebrata,—since we now find that they are composed each of two tracts, as in vertebrated animals,—it is interesting to observe that these two cords, and the tracts of which they are composed, bear the same relative position to the viscera and to the exterior of the body as in Man and other Vertebrata. Thus the cord which runs along the ventral surface in Articulata has its motor tract nearest to the viscera (*a*), or most internal, the same as in the human subject; while the sensitive tract, which possesses the ganglia, lies along the under surface of the cord, and is nearest to the exterior of the body, just as the sensitive tract with its ganglia in Man lies nearest to the cutaneous or external surface. It will thus be seen that the two tracts maintain the same relative position with regard to each other, as well as to other parts of the body, in both divisions of the great kingdom of animated nature, whether the actual situation of the cords be along the dorsal or ventral surface of the body. This being the case, it leads us to consider the propriety of the terms *anterior* and *posterior tracts* or *columns*, as applied to the motor and sensitive tracts of the nervous system, and whether it would not be advisable entirely to abandon these terms, and designate the two columns *external* and *internal*, the sensitive the external, and the motor the internal column, since these terms would be strictly applicable to the situation or position of the columns in all classes of animals.

Perhaps it may at first appear doubtful whether this be really the case, since the large cerebral ganglia which give origin to the principal nerves of sense in Invertebrata are situated above the œsophagus towards the dorsal surface of the animal, while the cords themselves, and the ganglia which give origin to the nerves of motion and sensation simply, as well as those which supply the organs of manducation, are situated below it, along the ventral surface of the animal. Upon close examination it will be found that when the motor column in passing from the thorax to the head has arrived at the crura which descend from the brain on both sides of the œsophagus, it appears to wind round to the outer surface and unite with the base of the antennal nerves, where the column appears to terminate. It is in the median line above and between the two double cords that the transverse nerves originate (*b*), as described in my former paper; and these also unite with the nerves to the antennæ by very small filaments. This inclines me to consider them as forming part of one great system of nerves, which are more of an involuntary than of a voluntary character. Of this great system the sympathetic nerves doubtless form a part, of which the transverse nerves perhaps may be only a peculiar modification. It is a remarkable fact, that while the muscles of the wings are supplied with nerves which in every stage of the insect's existence originate by double roots, one of which is derived from the motor tract of the cords before it arrives at a ganglion, and the other both from a ganglion of the sensitive tract and from the motor tract which passes over it, they are also supplied with large nerves from the transverse series, as may be best seen in the larva, long before the organs unto which they are given are called into activity. But this is not the case with the muscles of the legs, which are supplied only with very minute filaments from the transverse series, in addition to their compound or moto-sensitive nerves. The reason for this difference in the distribution of the nerves to the wings and legs is clearly on account only of their difference of function, the wings being more directly concerned than the legs in the acts of respiration. Professor MÜLLER\* has recently thrown out some valuable hints with regard to the nature of these transverse nerves; he seems to consider them as peculiar nerves which combine the animal with the organic functions, not distinctly sympathetic nerves nor nerves of entirely voluntary motion. I am greatly inclined to lean to this opinion. It is evident that they are not simply the sympathetic system, because they are given so much to the muscles and tracheal vessels, while but very few filaments go to the viscera. I am less inclined to regard these nerves as the analogues of the true sympathetic, on account of their great size in certain insects, and because also it has been stated by DE SERRES† and Dr. GRANT‡ that a series of ganglia exists on each side of the alimentary canal, which appears to be independent of the transverse nerves. I must acknowledge, however, that I have been unable to trace this series beyond the

\* MÜLLER'S Archiv für Anatomie, &c., No. 1. 1835, pp. 81, 84.

† Paper on the Sympathetic Nerves of Insects.

‡ Lecture on Comparative Anatomy. Lancet, 1834, vol. ii. p. 515.

anterior lateral ganglia, which are contained within the head, or first segment, and are analogous to the superior cervical ganglia; and Professor MÜLLER, in his paper upon the Sympathetic or Visceral Nerves of Insects, has expressed his doubts with regard to its existence as described by DE SERRES. MÜLLER regards the nerve which I have described on a former occasion as the vagus, as analogous to the sympathetic; but there are many points which seem opposed to this opinion. The vagus, or recurrent nerve of LYONET, is exceedingly small in almost every insect when compared with the size of the organs unto which it is distributed, especially when we compare those organs, and the nerves which supply them, with the corresponding parts of the human body. Besides which I have never been able to trace the nerve along the alimentary canal beyond the middle portion of the stomach, where it seems to be lost in the same manner as in Man and other Vertebrata.

With regard to the cords themselves, it was long ago suggested by WEBER that the ganglia, which we now find to exist entirely in the sensitive tract in insects, are analogous to the intervertebral ganglia of Vertebrata. Hence the analogy between the spinal cord of Vertebrata and the abdominal cords in Invertebrata is very nearly proved. The very great analogy between the origin, course, and situation of the vagi nerves in Man, and the corresponding one in insects, clearly demonstrates the identity of the structures. CARUS\* has made some observations which lead us to consider whether the œsophagus and crop in some volant insects are not somewhat concerned in the function of respiration, since it is well known that every part of the alimentary canal is profusely supplied with tracheal vessels, and especially when we remember that the vagus is the chief nerve of the organs of respiration in Man. I shall therefore go more particularly into a description of this nerve in insects.

In all lepidopterous insects it has two distinct origins, one from each crus, which descends from the base of the cerebral ganglia or lobes of the brain. These origins are analogous to the two vagi nerves in Man, but instead of continuing separate and passing down one on each side of the œsophagus, they pass at first a little forwards and inwards, and unite above the palate, where they form a ganglion. Here also we have some analogy with the nerve in Man. The vagus nerve, after its junction with the spinal accessory, passes forwards and out of the skull through the foramen lacerum posterius, and there forms a slight enlargement almost precisely corresponding in situation to the point above the palate and pharynx, where the ganglia would have been situated on the nerves had the two vagi nerves in Man been united. From the ganglion thus formed by the union of the two roots of the vagus nerve in insects, the two approximated origins thus forming one trunk pass backwards along the median line of the œsophagus beneath the anterior portion of the dorsal vessel. A little behind the brain the vagus is united by filaments with the anterior lateral or cervical ganglia, which are analogous to the superior cervical of the sympathetic in Man. Here there is an analogy between the union of these ganglia and the vagus in insects, and the

\* Comparative Anatomy, translated by GORE, vol. ii. p. 166.

corresponding ganglia and vagus in Vertebrata. The vagus nerve then passes along the median line of the œsophagus in close relation with the anterior or aortal portion of the dorsal vessel, which may be looked upon as the two carotids of Vertebrata united. The nerve lies between this portion of the vessel and the œsophagus, as between the carotids and lateral parts of the œsophagus in Vertebrata. A little before the vagus arrives at the cardiac portion of the stomach in insects it divides again into two parts, and very often at its point of division again forms a ganglion. This is the case in the *Meloë*, LINN., and some other genera. These two parts are divided into many others, which are distributed over the sides of the stomach, so that even in its ultimate distribution in insects the nerve still bears analogy to its distribution, and its division into many branches around the œsophagus and cardiac extremity of the stomach in Man and the higher Vertebrata. In *Crustacea* the nerve closely resembles that of insects, but approaches even nearer in its resemblance to that of Man. It is given almost entirely to the stomach, at the cardiac portion of which it forms a ganglion, and then divides into two branches, each division being subdivided into four portions, which are distributed around the stomach. Only a few filaments from these portions unite with some very fine nerves, which probably are the sympathetic, and which are given to the highly developed liver in these animals.

The minute distribution of the transverse and moto-sensitive nerves deserves particular attention. It is known that a ganglion exists in the sensitive tract of the cords in each segment, and that immediately anterior to this ganglion, on the dorsal surface of the cords, there is also a set of the transverse nerves (*c*). Each set of transverse nerves at the point of divergence from its longitudinal portion, which lies above and between the cords, forms a triangular plexus (*b*), in which the transverse fibres are observed to be continuous from one side of the body to the other, joined by the longitudinal ones, and thus form the plexus. The first branch from each set or plexus of transverse nerves is very small, and passes, as formerly described\*, over the outer margin of the next ganglion (*a*), and then converging to the median line unites with its fellow of the opposite side to form the longitudinal tract (*d*), after each fibre has received a few filaments from the upper or motor surface of the cords. Hence these nerves are of mixed character, and contain some voluntary motor fibrils. The second branch of the transverse nerves (*e*) is given off on the inner side of the smaller rectus, and unites with the moto-sensitive nerve from the ganglion and motor tract of the cords (*f*). The transverse nerve then passes diagonally outwards and forwards over the smaller rectus, near the external margin of which it gives off its third branch (*g*); this passes at first forwards and outwards until it arrives at the insertion of the preceding small rectus. It then passes along the upper surface of the middle of the rectus, unto which it distributes minute branches, until it arrives at about the middle of the muscle. It then sends forward a small branch to the anterior extremity of the muscle (*h*), while its main trunk bends directly inwards to unite

\* Philosophical Transactions, Part II., 1834, p. 410.



as will presently be shown, with a branch from the great moto-sensitive nerve. This union is exceedingly interesting, and proves that some of the nerves, at least, terminate in loops, which unite with portions of other nerves, according to the views of some of the German physiologists. The fourth branch also is an exceedingly interesting one, from its uniting in a similar manner with a branch from another moto-sensitive nerve. It is composed of fibres which are approximated to those of the transverse trunk, some of which passing from without inwards, and others from within outwards, form a little triangular plexus (*i*), similar to the one before described, and then unite to form the fourth branch of the transverse nerve. This branch passes directly forwards along the inner margin of the great rectus, and having arrived at the insertion of the muscle, it gives off a filament, which, dividing again into two portions (*j*), passes directly outwards, and is given to the greater recti at their insertion. The nerve then passes forwards to the external margin of the greater oblique, unto the lower portion of which it gives many filaments, and also to the second and third oblique, and to the triangularis, and then unites with the second, or inner division of the second pair of moto-sensitive nerves of the cord (*k*) in the preceding segment. The fifth branch of the transverse nerve passes off from the trunk a little more externally (*l*), and is given to the visceral surface of the greater rectus, and to some large tracheæ which are distributed over it. The transverse nerve then gives off a few small branches to the rectus, while its main trunk passes outwards until it arrives at a tuft of tracheal vessels which arise from the longitudinal trachea opposite to a spiracle (*m*). It then divides into two principal branches, one of which passes on each side of these tracheæ, giving off many branches. Some of these from the anterior branch pass inwards along the course of the tracheæ towards the alimentary canal, others forwards to the transverse lateral muscles, unto which they give filaments, and others upwards to the dorsal recti, unto which they are also distributed, while some of their ultimate branches appear to be given to the dorsal vessel. The posterior division of the nerve in like manner gives filaments to the tracheæ which arise opposite to the spiracle. A small branch joins with the trunk of the great moto-sensitive nerve (*n*), which crosses the trachea posterior to the spiracle. Another branch passes backwards, and dividing into several branches is given to the lateral oblique and lateral rectus muscles (*o*), and a fourth set passes onwards along the visceral surface of the dorsal rectus and to the dorsal vessel.

All the muscles unto which these nerves are distributed, besides being concerned in respiration, are necessarily concerned in the voluntary motions of the insect, and consequently it is necessary that they should be supplied with voluntary nerves, as well as with those just described, which are presumed to be of mixed function. This, it will be seen, is actually the case.

The first or chief pair of nerves from the moto-sensitive columns in each segment (*f*), is composed of one portion from the ganglion of the sensitive tract, and one from the motor which passes over it, and, after receiving a small filament from

the transverse nerve (*e*), passes outwards over the smaller rectus, at the outer margin of which it gives off its first branch (*p*), which is directed backwards. It then passes between the third and fourth oblique, and gives off its second branch (*q*), which is directed forwards, and a little further outwards its third (*r*) and fourth (*s*), which are directed backwards. The trunk of the nerve then crosses the longitudinal trachea, and unites with a short nerve from the posterior division of the transverse nerve (*n*). It then divides into two branches (*t*), which pass upwards between the dorsal recti and oblique muscles, where they again divide into many branches. About midway across the dorsal recti some of the branches interweave with each other, and form a small plexus (*u*) before they are distributed to their proper muscles. It is the first two divisions of this great nerve which particularly claim our attention. The first division (*p*) passes backwards beneath the greater rectus, and divides again into two branches. The anterior one (*v*) is given to the four oblique muscles, and to the under surface of the rectus, which are thus shown to be supplied by two sets of nerves. The second division passes backwards and is again subdivided; the posterior division being given to the under surface of the smaller rectus, and to the lower portion of the great oblique, while its termination (*w*) is continuous with a portion of the second branch of the transverse nerves (*h*). Some of the branches of this nerve pass between the triangular and second oblique muscles (*x*), and are given to the latero-abdominal. The second branch of the main trunk of this nerve (*q*) passes obliquely forwards and outwards beneath the great oblique, and gives off first a small branch to the transverse abdominal muscles (*y*), and a little further on a second branch, one portion of which is also given to the transverse and latero-abdominal muscles (*z*), and another which passing more directly outwards supplies the latero-abdominal (31) and the oblique great constrictor of the spiracle (25), and divides behind the spiracle into two terminal portions, one of which is given to the retractor valvulæ (27), and the other, which passes forwards, to the transverse lateral muscles (24), which, as before stated, are supplied by two distinct sets of nerves. The divisions of this last portion of nerve are particularly interesting. Before dissecting these nerves I had conceived that the great constrictor of the spiracle and retractor valvulæ muscles were probably supplied by the transverse nerves, and hence was much surprised to find that they were supplied from the great moto-sensitive nerve from the ganglion of the cords, by which they are thus endowed with voluntary power and sensation. But upon reflection it will be seen that this ought really to be the case. To enable the insect to make a forcible expiration and close its spiracle, which is evidently an effort of the will, the great constrictor of the spiracle ought to be endowed with voluntary power. On the other hand, since the insect has a voluntary power of closing, it must also have a similar power of opening the orifice, and consequently the retractor valvulæ ought necessarily to be supplied from the same source. There are, however, a few filaments given from the transverse nerves to these muscles, and to the orbicular which surrounds the spiracle. The remaining portion of the

trunk of this nerve passes forwards and outwards, crosses the retractor of the spiracle, and then gives off its third branch (32), which is almost immediately again divided, and sends one portion backwards to the transverse abdominal (17) and anterior abdominal (18), and the other forwards to the transverse lateral muscles (23). The remaining portion of the nerve continues its course over the transverse lateral, and terminates in the muscles of the back.

The second or oblique moto-sensitive nerve (33) from the cords and ganglia is much smaller than the first, the one we have just described. It passes diagonally outwards and backwards, and divides into two principal branches. The first passes outwards, and is given to the latero-abdominal muscles, which contract the diameter of the segment. One portion of the second branch supplies the triangular and transverse median muscles, while the other (*k*) passes downwards and outwards and unites with a portion of the third branch of the transverse nerves (*i*), as before stated.

From this distribution of the nerves it is evident that some of the muscles are supplied from two sources, and it can hardly be doubted that these have distinct functions. The remarkable fact that the transverse nerves appear almost exclusively to supply the tracheæ, while the moto-sensitive, which come from the motor tract and ganglia, and communicate volition and sensation, supply the muscles, even of the spiracles, cannot escape our observation as a striking proof that these nerves are of distinct functions. When we connect these facts with that of the longitudinal portion of the transverse nerves in each segment deriving a few filaments from the motor surface of the cords, and with that of filaments from the transverse nerves being distributed to some of the muscles in addition to nerves derived from the cords and ganglia, we can scarcely hesitate to assent to the opinion that while the transverse nerves connect the voluntary with the great organic functions of the body, they are more subservient to the latter than to the voluntary or animal powers.

*The Manner in which Respiration is performed.*

It has been shown that in every act of respiration in insects nearly all the muscles and nerves of each segment of the body are brought into consentaneous action, as the muscles of the chest and ribs in vertebrated animals, like which the insect is able to make either a forcible expiration, as during pain, and perhaps also during transformation, or can take a forcible inspiration at the instant of any sudden exertion. The manner in which the air is renewed in the trachea has excited some inquiry, but no satisfactory explanation of it has yet been given. Some have supposed that the dilatations and contractions of the dorsal vessel contribute towards it, others that simply the opening and shutting of the spiracles, the extension and contraction of the body, the presumed elasticity of the air-sacs, or the sliding of the segments one over the other, may be the means of effecting it\*. But neither of these actions could alone induce a current, or succession of currents of air to be sent over the whole body,

\* CARUS, Introduction to Comparative Anatomy, vol. ii. p. 167, translated by GORE.

through the ramifying and anastomosing tracheæ, sufficient for the purposes of respiration, which is probably the result of several combined actions. The experimental fact observed by REAUMUR, that the anterior pair of spiracles is the most important to the insect, connected with that of the gradual obliteration of the last two pairs during the changes to the perfect state, and the great extent to which the anterior spiracles are developed as the insect approaches that condition, lead us to conclude at once that it is chiefly through the anterior spiracles that respiration is performed. The action of the *retractores spiracula* muscles necessarily tends to contract the segments and close the spiracles, and thus, as it were, pump on the air through the longitudinal tracheæ towards the anterior or thoracic ones; while the relaxation of these muscles, and of the other oblique and longitudinal ones in each abdominal segment during the time the muscles of the thorax are in action, must naturally tend to enlarge the capacity of the body and induce an act of inspiration. Indeed we have full proof that respiration is performed by the alternate contraction and relaxation of the abdominal muscles in what takes place in Orthopterous, Hemipterous, and many Coleopterous insects. CARUS has well remarked, that the abdominal segments, particularly in *Locusta*, are alternately elevated and depressed, like the ribs of Vertebrata; and every one must have observed the same thing in the larger *Bombi*, when fatigued, upon alighting after flight, and when excited. The contractions and relaxations of the muscles, and consequently the acts of inspiration and expiration, are then short and quick in proportion to the degree of excitement, which is sometimes so great that the whole abdomen is alternately extended and retracted just as the flanks and ribs of the racehorse alternate with each inspiration after a long and severely contested struggle on the course. In the *Gryllus viridissimus*, LINN., when excited I have counted thirty-seven contractions, corresponding to as many respirations, per minute, and these were precisely analogous to similar acts in Vertebrata. Thus several short contractions take place in regular succession at stated intervals, and these are followed by one more long and powerful than the rest. A slight pause then ensues, and the short contractions again commence, until they are followed at a certain interval by another long one, which is evidently a full inspiration, and takes place at no stated interval. When the insect is very much excited the interval between the long inspirations is greater, and the inspirations when made are more full and powerful. This view of the manner in which respiration is performed in insects is supported by the test of experiment.

If one of the larger moths be submerged in water, a few bubbles of air will be seen to arise from all the spiracles on each side of the body, but chiefly from the first, second, and third pairs. These bubbles diminish in size as we proceed towards the posterior extremity of the insect, the first and second pairs being the largest. During the changes of the insect these spiracles are greatly increased in size, and often considerably altered in form, while the spiracles and tracheæ in the posterior portion of the body are greatly diminished, and the anal pair which existed in the larva is

entirely obliterated. The quantity of air expired through the different orifices must therefore be greater at the anterior than at the posterior ones. But if one of the larger Humble-bees (*Bombi*) be placed in water, and allowed to remain completely submerged until it has become nearly asphyxiated, the fact will then be still more apparent. At first there will be two large bubbles expired from the anterior spiracles, on each side of the trunk, at each longitudinal contraction of the abdominal segments, which corresponds to each expiration; but as the insect becomes more completely asphyxiated, the bubble of air will be only partially expelled from the spiracle, and again withdrawn at the entrance, without having escaped, at each longitudinal extension of the segments, which corresponds to each inspiration, while not a single bubble of air can be detected at the entrance of the posterior abdominal segments\*. It is evident from this that it is chiefly through the anterior spiracles that respiration is performed; and it may from hence be inferred that the manner in which the insect prepares itself for flight is exactly like that of birds under similar circumstances. At the moment of elevating its elytra and expanding its wings the anterior pairs of spiracles are opened in the act of inspiration, and the air rushing into them passes into the tracheæ of the whole body, distending the air-bags and rendering the insect of less specific gravity, so that when the spiracles are closed at the instant when the insect endeavours to raise itself in the air, it is enabled to sustain a long and powerful flight with but little expenditure of muscular power. This is the condition of respiration in the perfect insect. In the pupa, and still more so in the larva, respiration is performed more equally by all the spiracles of the body, and less particularly by those of the thoracic segments. But even in these conditions of the insect the bubbles expired from the three anterior pairs of spiracles are the largest, and consequently these spiracles are the most important ones. It is thus evident that in the larva state the condition of respiration is but little advanced beyond that of the higher Vermes, and that it is only when the insect has passed through all its changes that its respiration is similar to that of the more perfect animals, which the insect then greatly resembles both in external and internal conformation.

The quantity and rapidity, or activity, of respiration appear to bear some relation to the muscular power of the insect in a state of activity. All volant insects, and among these particularly the *Hymenoptera*, respire with a greater rapidity in a given space of time, and degree of atmospheric temperature, than terrestrial insects, and in their larva condition much less than in their perfect. In the common Hive-Bee, *Apis mellifica*, LINN., I have counted from one hundred and ten to one hundred and sixty contractions of the abdominal segments per minute when the insect has been

\* DEGEER appears to have made a similar observation, which he considered as expiration and inspiration, but the correctness of the opinion has been doubted by CARUS, vol. ii. p. 167. Mr. GOADBY has also noticed the contractions of the segments as analogous to acts of inspiration and expiration, but has not expressed an opinion respecting respiration being carried on chiefly through the anterior spiracles. See Medical Gazette, April 2, 1836.

much fatigued, while in the natural state, when the insect is undisturbed, the contractions of the segments, or acts of respiration, seldom amount to one half that number. In an extremely wild and irritable little bee, *Anthophora retusa*, STEPH., which dies from the most violent excitement and exhaustion in the course of an hour or two, after being captured and confined during summer, although plentifully supplied with food,—the acts of respiration are performed so rapidly that it is almost impossible to number them. On one occasion myself and a friend counted two hundred and forty in a minute.

The condition of respiration when an insect is recovering from a state of torpidity is very interesting. In the beginning of January, on a fine but cold windy day, upon examining one of my hives I found many bees which, having ventured abroad when the hive was disturbed, were lying torpid and completely motionless in a side box that was attached to the hive, when the temperature of the air was about 40° FAHR. I removed some of these to a room, the temperature of which was 60° FAHR., and they soon gave indications of reviviscence. The first visible signs of returning animation were slight twitchings of the tarsi, and feeble contractions of the abdominal segments, which gradually increased in frequency, but were at first very irregular. At two minutes after the first motions of the abdominal segments, and consequently after the acts of respiration were first perceived, the contractions gradually became more regular in their occurrence, and amounted to fifty-eight per minute. At the expiration of four minutes they amounted to sixty-three, at six minutes to seventy-two, at eleven minutes to eighty, at fifteen minutes to seventy-seven, at which time the insect began to move the whole of its limbs. At eighteen minutes they amounted to eighty-five, at twenty minutes to eighty-seven, at twenty-five minutes to eighty-four, at thirty-three minutes to one hundred and two, and at thirty-six minutes to one hundred and five; and when the insect was perfectly recovered, and had been for some time in a state of activity, the number of its respirations amounted to one hundred and sixty per minute. At thirty-three minutes the insect had regained its power of locomotion, and began to move about, and its respiration, which had then become more quiet and regular, was still more frequent than in a state of perfect health, when it seldom exceeds forty inspirations per minute.

It is in the pupa state that insects respire less frequently than in any other, and it is in this state that I have been able most distinctly to observe the action of the spiracles. When the insect has remained in the pupa state for a few weeks, in a low temperature, it passes into a complete state of hybernation, and its respiration, as I shall presently show, is almost entirely suspended; but when the insect has been kept in a temperature of 60° FAHR. or upwards, it respire very freely, and the action of the spiracles in the pupa of *Sphinx ligustri* may sometimes be observed by means of a microscope. There are in general about three contractions of the spiracles per minute, the intervals between which are very regular. A perfectly healthy and vigorous pupa always closes its spiracles whenever any irritating or obnoxious

substance is brought into contact with them, which distinctly proves the possession of a voluntary power over the muscles connected with them, and which, as before shown, are supplied from the moto-sensitive columns.

*Quantity of Respiration.*

The very important fact established by Dr. EDWARDS in the higher animals, that a greater quantity of oxygen is required in the adult state in proportion to the capacity of the respiratory apparatus than in the earlier or infant condition of the animal, and that in a state of hybernation less even is required than in the infant state, is equally true as regards also the air-breathing Invertebrata, particularly the class of insects. The larva of *Ichneumon Atropos*, STEPH., concealed within the body of the larva of *Sphinx ligustri*, LINN., and preying upon its substance, although provided with minute spiracles which lead into extremely delicate tracheæ distributed through its body, and doubtless maintaining a certain degree of respiration, requires not a twentieth part the amount of atmospheric air for its support which it requires in its perfect condition. The larvæ of the wild bank bees, *Anthophora retusa*, STEPH., and *Eucera longicornis*, STEPH., and of many others, confined in their cells in the earth; of the Sand Wasps and Spheges, buried deeply in the soil; of the *Cerambyces* and *Ptinidæ*, and other wood-boring insects; and of the *Scarabæi*, *Lucani*, *Tipulæ*, and *Muscæ*, many of which live in the most noxious and unaerated places, can exist for a very long time in situations in which the same insects in their perfect state would soon perish. Hence it is clear that a smaller quantity of air is required for the support of these insects while larvæ than when they have become perfect. The quantity of air required for the support of the same tribes of insects varies in like manner in the different species.

In the summer of 1832, at the suggestion of my friend Dr. MARSHALL HALL, I was led to inquire whether the quantity of respiration in insects bears any relation to the comparative irritability of the muscular fibre in the different genera and states of the same tribes of insects; and I was afterwards led to inquire more particularly into the exact amount of respiration in different insects, and different states of the same insects, for the purpose of ascertaining what relation, if any, subsists between the quantity of respiration and natural temperature of body in these animals. Although I was unable at that time to ascertain the exact amount of respiration in the different states and species, owing to various causes, such as the variations of the thermometer, the degree of excitement or quiescence of the insect, and consequently the uncertain amount of air consumed, and quantity of carbonic acid gas produced during the observation, yet the results gave a near approximation to the truth, and enabled me to form an opinion respecting the real amount in each observation when made under similar circumstances. The observations were made in the following manner. When a single specimen was employed the cubic bulk of the insect was first ascertained, and the insect was then confined in an accurately closed stoppered phial of known

capacity, the time of day and temperature of the atmosphere being noted. After a certain period the stopper was carefully withdrawn under, and the phial was allowed to remain inverted in lime-water for about an hour. The quantity of carbonic acid gas, and consequently a near approximation to the real amount of respiration in a given time, was thus indicated by the absorption which took place,—proper allowance being made for the variations of the thermometer, and for other circumstances, which occurred during the period of observation. Although it must be evident that this mode of ascertaining the quantity of respiration is open to objections, it is sufficiently accurate to enable us to form a comparative view of the amount in different states and insects.

The quantity of respiration during a given period is very greatly influenced by the insects being either in a state of activity or quiescence, which explains the apparent discrepancy of some of the results, as shown in the accompanying Table.

TABLE I.

Exhibiting the quantity of carbonic acid gas excreted by different species of insects in their different states, and under different circumstances.

No.	Name of insect.	State.	Specimens.	Bulk.	Capacity of phial.	Hours inclosed.	Temperature.	Carbonic acid produced.	Remarks.
1.	<i>Sphinx ligustri</i> .....	Larva	1	0.13	1.96	5	69 to 71	0.430	} During the day, soon after entering its last larva skin: August.
2.	<i>Sphinx ligustri</i> .....	Larva	1	0.15	3.16	5	69 to 71	0.431	
3.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	2.68	147	47.5 to 47.5	0.210	} During the day, in the same condition. March 6, confined in the open air.
4.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	1.88	95	52.5 to 58	0.230	
5.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	2.03	156	46 to 46	0.190	} Confined in my sitting-room, March 6. Confined in the open air, March 12.
6.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	1.94	156	46 to 46	0.190	
7.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	1.88	180	58 to 58	0.400	} Confined in my sitting-room, Mar. 12. March 25, has been long kept in high temperature.
8.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	2.34	194	61.5 to 59	0.345	
9.	<i>Sphinx ligustri</i> .....	Pupa	1	0.29	1.88	194	61.5 to 59	0.310	} Brought from exposure in open air to higher temperature. Confined in open air on the ground, March 25.
10.	<i>Sphinx ligustri</i> .....	Pupa	1	0.28	1.89	210	48 to 48	0.235	
11.	<i>Papilio urticae</i> .....	Larva	3	0.09	1.14	12	70 to 66	0.120	} Larvæ not full grown.
12.	<i>Papilio urticae</i> .....	Larva	3	0.07	1.14	11	68 to 78	0.140	
13.	<i>Papilio urticae</i> .....	Larva	3	0.07	1.14	7	65 to 74	0.110	} Very active, July.
14.	<i>Papilio urticae</i> .....	Larva	3	0.07	1.14	6½	75 to 69	0.140	
15.	<i>Papilio urticae</i> .....	Pupa	5	0.10	1.96	48	67 to 78	0.130	} Two days old.
16.	<i>Papilio urticae</i> .....	Pupa	3	0.08	1.14	22	74 to 84	0.160	
17.	<i>Papilio urticae</i> ..	Pupa	3	0.08	1.14	10	74 to 69	0.050	} Three days old.
18.	<i>Papilio urticae</i> .....	Pupa	3	0.08	1.14	10	69 to 69	0.040	
19.	<i>Papilio urticae</i> .....	Pupa	3	0.08	1.14	10	67 to 67	0.041	} During the night.
20.	<i>Papilio urticae</i> .....	Perfect	3	0.07	1.14	16½	79 to 82	0.200	
21.	<i>Phalæna vinula</i> .....	Pupa	1	0.11	2.34	257½	54 to 58	0.270	} Just taken from its cocoon, March 6. Same specimen used, March 25.
22.	<i>Phalæna vinula</i> .....	Pupa	1	0.11	2.68	194	61.5	0.363	
23.	<i>Phalæna vinula</i> .....	Perfect	1	.....	2.68	12	63 to 63	0.480	} Active, April 23.
24.	<i>Phalæna vinula</i> .....	Perfect	1	.....	2.68	12	63 to 63	0.490	
25.	<i>Bombus terrestris</i> .....	Perfect	1	0.035	2.03	1	60	0.255	} More active, April 23.
26.	<i>Bombus terrestris</i> .....	Perfect	1	0.055	2.03	1	60	0.345	
27.	<i>Bombus terrestris</i> .....	Perfect	1	0.055	2.03	20	59	0.305	} Just captured, active, April 6.
28.	<i>Bombus terrestris</i> .....	Perfect	1	0.055	2.03	3½	60 to 59	0.120	
29.	<i>Anthophora retusa</i> .....	Perfect	1	0.023	1.88	1½	64	0.255	} Just captured and fed, very active.
30.	<i>Anthophora retusa</i> .....	Perfect	1	0.023	1.88	1½	66	0.330	
31.	<i>Geotropes vernalis</i> .....	Perfect	1	0.11	2.68	12	63 to 62	0.215	} Resting during the whole observation. Very slightly active.
32.	<i>Geotropes vernalis</i> .....	Perfect	1	0.11	2.68	26	60	0.480	
33.	<i>Carabus cancellatus</i> ...	Perfect	1	0.4	1.94	20	60 to 62	0.400	} Active.
34.	<i>Carabus cancellatus</i> ...	Perfect	1	0.4	1.94	54	60 to 60	0.430	
35.	<i>Chrysomela tenebricosa</i>	Perfect	4	0.4	2.34	17½	58 to 57	0.340	} Moderately active.
36.	<i>Meloe violaceus</i> .....	Perfect	1	0.4	2.34	25	63 to 63	0.190	



TREVIRANUS has very justly observed\*, that the quantity, or I should rather say the activity of respiration in insects, is increased with the increase of atmospheric temperature. At the same time the law which has been established by Dr. EDWARDS with regard to the respiration of vertebrated animals, is equally applicable to insects, namely, that supposing the *activity* of respiration to be exactly of the same degree at two extremes of atmospheric temperature, say 32° FAHR. and 60° FAHR., there would be a greater quantity of oxygen consumed at the lower than at the higher temperature. It is necessary to bear all these circumstances in mind, and also the comparative size of the insect, in estimating the amount of its respiration. Thus the larvæ of Lepidopterous insects appear to respire a greater quantity of atmospheric air in a given time than the perfect insects or pupæ; but it must be remembered that they are in general very much larger in bulk, sometimes even double that of the perfect insect, and consequently consume a greater quantity of air. But if we examine larvæ which are of the same cubic bulk as their perfect insects, we shall find that, provided they continue in a state of activity, the respiration of the perfect insects will be much greater than that of their larvæ, as is shown in the observations on *Papilio urticae*, LINN. in its different states, Table I., No. 11 to 20. It is there seen that the greatest amount of respiration is during the perfect state, and that the period when an insect which undergoes all its changes during a few weeks in the summer has the lowest degree of respiration, is about one or two days after it has entered its pupa state, as shown in the accompanying Table, No. 15. This is the condition of respiration during summer, when all the changes in the insect are continuous. The observations referred to in the Table were made upon larvæ which had not attained their full size, No. 12 to 14. But if a larva has arrived at its full size when the observation is made, it then appears to respire much more in a given time than the perfect insect. But this is not really the case. The observation is illusive, and arises, first, from the larva being almost always in a state of activity, and consequently having a more rapid consumption of oxygen, and next because it is frequently at least two thirds larger than the perfect insect. Thus the full-grown larva of *Odonestis potatoaria*, STEPH., is about .26 of a cubic inch in bulk, while the perfect insect is not more than .10. When the larva and perfect insect of this species were confined separately in glass stoppered phials of the same dimensions, 1.14, at the same temperature, 66° FAHR., the larva became asphyxiated in nine hours, while the perfect female was still living and vigorous at the expiration of twenty-four hours. In this case the larva was almost constantly in motion, while the perfect insect was quiet and resting. On a *prima facie* view of this observation it would appear that the larva respire a greater quantity of air, compared with its bulk, in a given time, than the perfect insect. It is a well established fact, that among the higher animals respiration is at its minimum during sleep. It is neither so frequent nor so voluminous, and consequently there is less oxygen consumed. This has been long known with regard to the human species; but, as shown

\* Lancet, vol. ii. 1835, p. 456.

by Dr. HALL\*, is more decidedly the case in the hybernating Mammalia; and it is exactly like these in insects, in which, as will presently be shown, respiration is almost entirely suspended at certain periods.

It generally happens, that while we are making observations upon larvæ they are in constant activity, and consequently they then consume the greatest amount of oxygen; while the perfect insect, independently of its being two thirds smaller in bulk, is generally in a state of complete inactivity, at rest or sleeping, and then consumes only its smallest proportion of oxygen. Besides this, it is probable that the very confinement of the perfect insect in a given quantity of air, insulated from external currents and sudden changes of temperature, may induce a more complete state of rest, and thus be the means of reducing the respiration still lower than it would otherwise have fallen, and still further prevent the necessity for a renewal of atmospheric air in the phial. A female specimen of *Bombyx Caja*, whose cubic bulk was about .09, confined in a phial of 1.14 capacity at a temperature varying from 63° to 71° FAHR., was still living and vigorous at the expiration of eighty-four hours; but during this time the insect was almost constantly in a state of inactivity. There is the same disposition in perfect butterflies (*Papiliones*) as in moths to become inactive when placed in confinement. After having been confined for a few minutes, and endeavouring to escape, they gradually become quiet, and their respiration is diminished. In order to prove distinctly that the quantity of respiration depends upon the degree of activity or quiescence of the individual insect, I confined a female *Bombus terrestris*, STEPH. (Table I. No. 28.), immediately after the insect was captured, in a glass-stoppered phial of about two cubic inches capacity, at a temperature of 60° FAHR. It continued in a state of violent activity, and in one hour evolved 0.345 of a cubic inch of carbonic acid gas; while the very same insect, when confined at nearly the same temperature (59° FAHR.) for twenty-four hours on the following day, during the whole of which time it was in a state of perfect rest, evolved only 0.305 of a cubic inch, which was not one twentieth part of the amount produced in a state of activity, although the insect had been fed immediately before commencing the observation.

The quantity of air deteriorated by an insect diminishes in proportion to the number of its respirations, and these diminish in frequency in proportion to the length of time it has remained in a state of quiescence. I had full proof of this during the above observation on the quantity of respiration of *Bombus terrestris*. Before noting the number of its respirations, the insect was allowed to remain at rest for about half an hour. At the expiration of that time the respirations were only fifty-eight per minute, and these were deep and laboured. At the expiration of one hundred and forty minutes, during the whole of which time the insect had remained at rest, its respirations were at the rate of only forty-six per minute: these were laborious and feeble, like those of an animal sinking into profound sleep. At the expiration of one hundred and eighty minutes, the respirations were no longer perceptible. Now in

\* Philosophical Transactions for 1832, Part I.

this very insect, soon after it was captured, the number of its respirations, in a moderate state of excitement, amounted to from one hundred and ten to one hundred and twenty per minute. I have recently observed the same difference between the number of respirations in a state of activity and quiescence in a female specimen of *Sphinx ligustri* in the perfect state. After the insect had been considerably excited in flight, it respired at the rate of forty-two per minute; but when it had remained at rest about seventy-five minutes, its respiration had subsided to only fifteen per minute.

This state of quiescence or profound sleep is the condition into which most insects fall at the close of summer, and in which they remain in their hybernacula during winter, when, if they be not disturbed, respiration becomes almost entirely suspended. This is the state of true hybernation. LYONET has stated his belief that the respiration of pupæ is *entirely* suspended for a very great length of time during winter; but his experiments with the pupæ of *Sphinx ligustri*, which led him to this statement, and which were made by merely covering the spiracles with soap-water, and watching with a microscope for the rising of bubbles, do not seem sufficiently precise and accurate to warrant the conclusion. For the purpose of ascertaining this fact, I made a number of observations in the year 1829 upon the pupa of the Sphinx, and have since repeated them under different circumstances. There are different degrees of respiration at the same season of the year in pupæ of different insects, which appear to have reference to the conditions in which the insects are placed in their natural haunts. When the *Sphinx ligustri*, which passes its winter in the earth, is examined in October or November, it gives most decisive proofs of respiration in the production of carbonic acid gas; but this is much smaller in quantity than that which is produced at the same period in a given time, and under similar circumstances, by the pupa of *Pavonia minor*, STEPH., which passes its winter in the open air, and is more readily exposed to the varied influences of the seasons. In both these insects the quantity of respiration is diminished as the winter advances. In December and January, respiration has subsided to its lowest state, and can be detected only with great difficulty while the insect remains undisturbed, but it does not entirely cease; for if at that period the pupa be brought into a warm atmosphere of 45° FAHR. or upwards, it soon begins to respire more freely, and if placed in water or alcohol, a string of bubbles will be expired from the spiracles at each contraction of the segments; thus proving that a more powerful respiration is immediately induced when the insect begins to be aroused from its hybernating slumbers. It is only when the medium in which the insect is living is below 32° FAHR. that respiration is very nearly suspended. On the 1st of January 1836 I repeated my observations, which had originally been instituted in the winter of 1829. I removed four pupæ of *Sphinx ligustri* from the ground, in which they had remained undisturbed for several weeks, and placed them in glass-stoppered bottles, three in one bottle and one in another, and buried them in the earth about four inches below the surface. The temperature of the soil at that depth was 37°·5 FAHR., and of the atmosphere a few inches above

the ground  $42^{\circ}8$  FAHR. For nearly a month before this the pupæ had been subject to the common influences of the season: there had been severe frost, the thermometer having sometimes sunk down to  $20^{\circ}$  FAHR. At the expiration of twenty-four hours the phials with the pupæ were removed from the ground, and their gaseous contents very carefully tested with pure lime-water, and gave the usual most unequivocal signs of respiration having taken place, but only in a slight degree. The temperature of the air a few inches above the ground was only  $31^{\circ}$  FAHR., that of the soil four inches beneath the surface  $35^{\circ}2$  FAHR.; so that it was clear the pupæ had continued to respire to within two or three degrees of the freezing-point, and perhaps even at very nearly that temperature. That the pupæ were still living and active, was proved by one of them once or twice contorting its abdomen when removed from the earth, before the stoppers of the bottles were withdrawn. The pupæ were then buried again as before, the temperature of the atmosphere and of the soil continuing respectively at  $35^{\circ}2$  and  $31^{\circ}$  FAHR. I then exposed another pupa in a stoppered phial on the surface of the ground for twenty-four hours. At eight o'clock on the following morning the thermometer stood at  $16^{\circ}5$  FAHR.; so that the pupa was then supporting a temperature of  $15^{\circ}5$  FAHR. below freezing. At the expiration of the twenty-four hours the temperature of the atmosphere had again risen to  $31^{\circ}2$  FAHR. and the phials were again examined. The temperature of the soil four inches below the surface was  $33^{\circ}5$  FAHR. In No. 3, which had been exposed on the surface of the ground, there was only the very faintest trace of carbonic acid gas, but sufficient to satisfy me that the pupa had respired. The phials Nos. 1 and 2 were then examined. In both there were incontestible proofs of the presence of carbonic acid gas; thus clearly indicating that the pupæ had respired freely at a temperature of  $33^{\circ}5$  FAHR., and in a slight degree even below  $32^{\circ}$  FAHR.

Although the pupæ employed on the above occasions had borne so low a temperature, they were not injured, since the whole of them have produced perfect insects\*. That a pupa which has been constantly exposed, for forty-eight hours, to a temperature of five degrees below freezing does not become frozen, I am fully satisfied, having once made a very careful examination in order to ascertain this point. The pupa was taken from its exposed situation with a pair of forceps, in order that it might not be touched with the fingers, and have its temperature increased, and a horizontal incision was instantly made with a sharp scalpel through the posterior part of its body, which separated the dorsal from the ventral surface. All the parts immediately collapsed when exposed to the open air, and the muscles were almost as tense as during a state of activity; the fat was of its usual whiteness, and the dorsal vessel was exactly as it appears during any other period, excepting that it was a little contracted in diameter, but its contents were fluid. When the body of the pupa was cut through, the fluid flowed as usual; but I could not observe any motion of the dorsal vessel, nor any

\* June 1836.

dilatation of the tracheæ; so that the circulatory and respiratory motions must have been very nearly, if not entirely, suspended. After the pupa had been held between my fingers for a few seconds, there was a slight contraction of the longitudinal muscles, resembling a respiratory effort, and I observed a motion commencing like the peristaltic motion among the viscera. I thought I could also observe a slight motion in the dorsal vessel. All this distinctly proved that the pupa had not been frozen. It is thus certain that a very great degree of cold can be borne by these insects without injury, and that during the time it is borne the respiration of the insect is very nearly suspended. But it is not merely a great degree of cold that can be borne by these insects without injury, but a great and sudden change of temperature, from a comparatively warm to a very cold atmosphere, as was shown in the observation on No. 3, above noticed; and even during that state the pupa will respire until the temperature has sunk below  $32^{\circ}$  FAHR. It is probable, that when the pupæ are remaining entirely undisturbed in their natural haunts, they respire much less, and that if the suspension of respiration really does take place, when it has once occurred it continues much longer than when they are removed from the soil and disturbed for the purpose of experimental observation, just as the sleep of the dormouse or bat will continue until the near approach of summer, although the animal is easily roused, and its respiration excited by external causes, even in the midst of winter. Yet it must be remarked, that when this takes place, whether the animal be one of the Mammalia or an insect which has arrived at its perfect state, it soon relapses again into its previous condition.

In order to ascertain the comparative amount of respiration in the same species of insect at the same period of the year in different degrees of temperature, I confined two pupæ of *Sphinx ligustri* in glass-stoppered bottles, inverted in a vessel of lime-water, and placed them on the ground in the open air, protected from the influence of the sun, and allowed them to remain for one hundred and fifty-six hours. During this time the temperature of the atmosphere was never lower than  $35^{\circ}$  FAHR., nor higher than  $58^{\circ}$  FAHR., being a range of  $23^{\circ}6$  FAHR. The temperature of the air at the time of inclosing the pupæ was at  $46^{\circ}$  FAHR., and it was exactly the same when the contents of the bottles were examined. The amount of carbonic acid gas produced by each of these pupæ was 0.19 of a cubic inch. This was between the 12th and 20th of March. At the time of inclosing these pupæ, I inclosed also another, which had previously been kept under precisely similar circumstances. This specimen was placed in my room, where the temperature during night was never lower than  $45^{\circ}$ , and during the day not higher than  $60^{\circ}$ , being a range of fifteen degrees. At the time of inclosing this pupa the temperature of the room was  $58^{\circ}$ , and it was at the same standard when the bottle was examined, which was at the expiration of a hundred and eighty hours. The quantity of carbonic acid gas amounted to 0.40 of a cubic inch, being nearly double the amount produced by either of the pupæ which were exposed to the open air; thus clearly proving that the relative quantity of respi-

ration in insects, as TREVIRANUS has recently remarked\*, very much depends upon the temperature of the air inspired, and also on the state of quiescence or activity in which the insect has been living. I made also other trials with other pupæ. I inclosed one pupa which had remained during the whole winter in the open air, and one which had been kept for several weeks in my room, in two stoppered phials, when the temperature of the atmosphere was  $61^{\circ}$  FAHR., and allowed them to remain for one hundred and ninety-four hours. During this time the temperature of the atmosphere varied scarcely more than eight or ten degrees, and both phials were examined at a temperature of  $59^{\circ}$  FAHR. The first specimen, which had remained in my room, produced 0.345 of a cubic inch of carbonic acid gas, while the other, which had been brought from the open air, produced only 0.310; a difference of thirty five thousandths less in the insect which had been exposed. Hence it is clear that respiration is less perfectly performed in those insects which are only newly aroused from their state of hybernation than in those which have been long kept in a state of excitement.

The amazing difference which exists in the quantity of respiration of pupæ and of perfect insects is strikingly exemplified in *Cerura vinula*, STEPH. (the Puss Moth). This insect, which it is well known is inclosed in a hard and impervious cocoon in the open air during its pupa state, is an admirable subject for experiment. On the 25th of March I inclosed a pupa, which had previously been several days removed from its cocoon, and consequently aroused from its hybernation, in a phial at a temperature of  $61^{\circ}5$  FAHR. At the expiration of one hundred and ninety-four hours it had produced only 0.363 of carbonic acid gas, which is considerably less than two thousandths per hour. On the 23rd and 24th of April I confined the same insect, twenty-four hours after it had escaped from the pupa state, and had become perfect, for twelve hours, at two separate times, when the temperature of the atmosphere was  $63^{\circ}$  FAHR. In one experiment it produced 0.480, and in the other 0.490 of carbonic acid, or at least forty thousandths per hour, and even during part of that time the insect was not in a state of activity.

It will thus be seen that the quantity of air deteriorated by an insect is regulated by various circumstances, independently of the natural habits of the species. When the pupa is in a state of complete hybernation, the respiration of the insect is at its minimum, while in the perfect insect, in a state of great activity, it is at its maximum. It is also evident that in making our observations the state of quiescence or activity, and the comparative bulk of the insect, in its different conditions, should be particularly attended to, or we may be led into errors whenever we attempt to compare the quantity of its respiration in its different states.

\* As noticed in the Lancet, vol. ii. 1835, p. 456.

*Duration of Life in different Media.*

An important subject connected with respiration is the capability which insects possess of supporting existence for a certain time in different media. It is a task of great difficulty to ascertain the precise length of time which different insects can continue in noxious media without being destroyed. We are so little aware of all the circumstances which affect the respiration of insects, that it is almost impossible to ascertain the precise moment when they cease to respire, or become asphyxiated; and it is still more difficult to be certain at what period, when respiration is suspended, life becomes extinct. We must therefore, in our experiments upon this subject, assume certain data, from which the comparative duration of life, under certain circumstances, may be inferred. With this view I have assumed four data, which mark very distinct conditions of respiration. The first is that moment at which, when confined in the noxious medium, the insect, by the violence of its struggles and efforts to escape, begins to appear to respire with great difficulty, and is becoming asphyxiated. The second is the moment at which it can no longer be observed to give signs of life by moving its limbs or the segments of its body, and when it may fairly be supposed that respiration is entirely suspended. The third is that moment at which, after being removed from the noxious medium, and exposed to the open air, the insect begins again to revive, its reviviscence being indicated by motions of its limbs or other parts of its body. The fourth is marked by the period when the insect is so far sufficiently recovered as to be again capable of locomotion. By comparing these circumstances in different insects, we obtain a comparative knowledge of the state of respiration as affected by different media.

In the months of July and August 1832, I made a series of observations on different insects with these assumed data, and I then found that the order in which the vitality of insects appears to be affected in different media is as follows: hydrogen, water, carbonic acid, nitrous acid gas, chlorine, and cyanogen, as shown in the accompanying Table; and I have since repeated the observations on several species of insects with similar results.

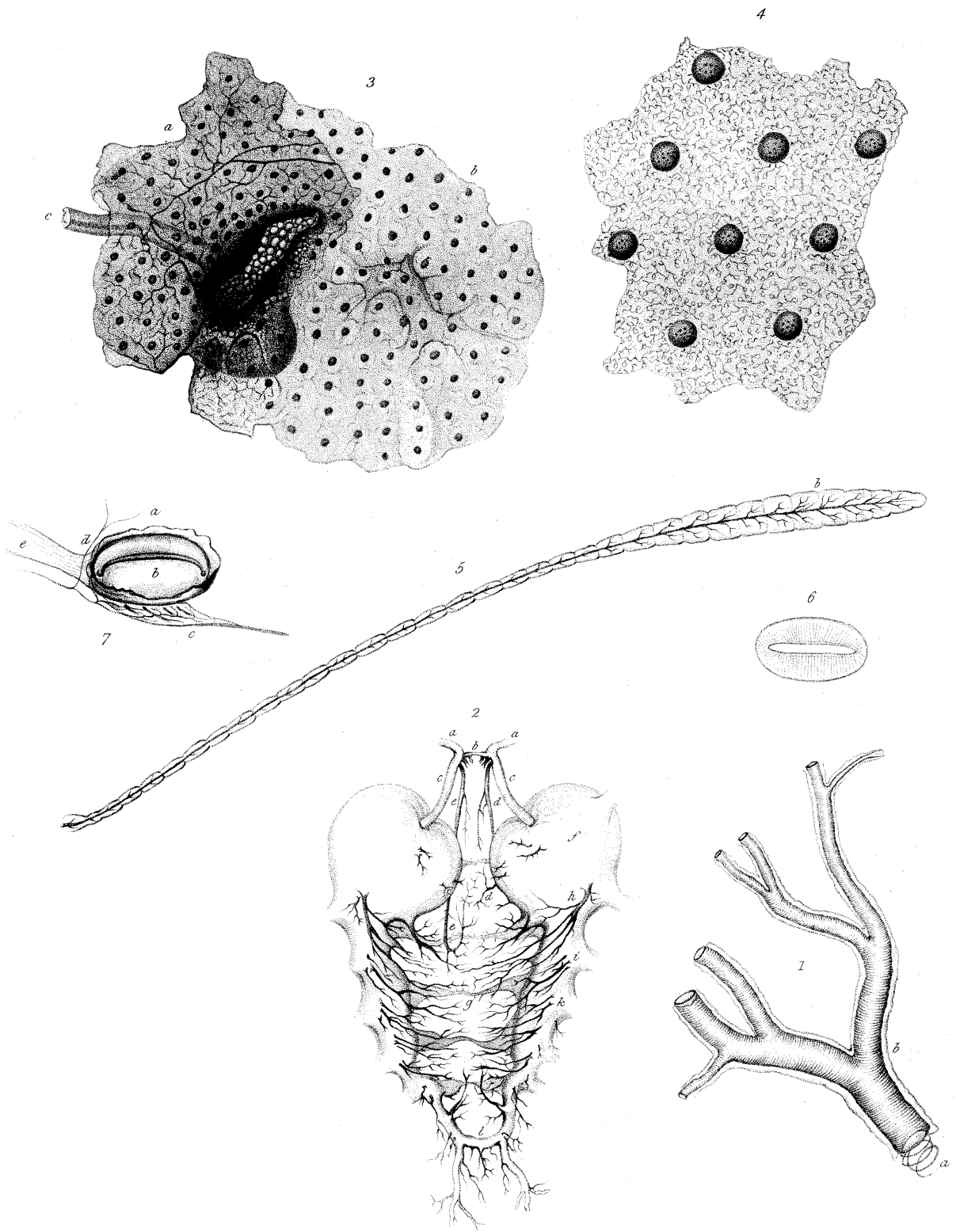




Some of these media affect respiration much sooner than others, which eventually are more fatal to the insect. Thus the larva of *Papilio urticae*, LINN., gave indications of life much longer in carbonic acid gas than in hydrogen, but was much longer in recovering from the pernicious effect of it when again exposed to the open air; while, on the contrary, the perfect insect became motionless much sooner in carbonic acid than in hydrogen. The larvæ of this insect were also much longer in recovering from submersion in water than from confinement in hydrogen, from the effects of which they began to recover immediately they were exposed to the open air. I invariably found that if hydrogen be diluted with only a very small proportion of its volume of atmospheric air, it is capable of being respired by insects for many hours. Insects generally recover from the effects of confinement for several hours in hydrogen, or water, upon exposure to the open air, although they may appear to have been completely destroyed. These media exert no noxious influence whatever upon the insect, but asphyxiate exactly as they affect vertebrated animals, simply by the absence of oxygen. Water, however, appears to have a twofold effect upon the insect, first by the absence of oxygen, and next by its depriving the insect of its natural heat, and lastly by the great degree of cold, or further abstraction of heat, produced by the evaporation which takes place from the surface of the insect when again exposed to the air for recovery. This latter circumstance may perhaps account for the greater length of time which elapses before reviviscence takes place after confinement in water than after confinement in hydrogen. A larva of *Papilio urticae*, LINN., which had been confined in hydrogen for more than twelve hours, began to revive in the course of two or three hours when again exposed to the open air, although it did not entirely recover its locomotive powers in a much longer period. A larva of the same species perfectly recovered in half an hour after being submerged in water for more than two hours. The larva of the common Drinker Moth (*Odonestis potatoaria*, STEPH.) perfectly recovered in one hour and a half, after being submerged for two hours and a half. The perfect female of the same species, after submersion for a similar length of time, perfectly recovered in less than an hour at a temperature of 73° FAHR. But this speedy reviviscence does not take place after confinement in carbonic acid, nitrous acid, and chlorine gas. Carbonic acid does not affect the respiration of insects so immediately as water, but ultimately it suppresses it much sooner; and although the individual gives signs of reviviscence rather sooner after confinement in carbonic acid than after submersion in water, it is much longer before it has completely recovered from its effects. Nitrous acid gas and chlorine seem at first to affect respiration about in the same degree, at least the symptoms are generally first apparent in about the same length of time. The first effects produced upon insects by these gases are generally observable in from five to ten seconds, although it is from fifteen to thirty seconds before the insect begins to make violent efforts to escape, while it seldom continues to give signs of animation for longer than from two to three minutes and a half. But the secondary effects of these gases are different.

Insects generally recover, although very slowly, after confinement in carbonic acid for a few minutes ; but they very seldom recover after confinement in a mixture of sulphurous and nitrous acid gas, or chlorine, which appear to affect them as direct and specific poisons. The rapidity with which these gases affect the respiration of insects depends upon the peculiar habits or natural constitution of the species. Thus insects accustomed to inhabit the open atmosphere, Lepidoptera and Hymenoptera, are affected almost instantaneously and perish quickly by these gases, while those which are accustomed to inhabit noisome places, as the Carabi and Geotrupes, are either not affected, or recover from their effects much sooner. A specimen of *Geotrupes vulgaris*, STEPH., when confined in a mixture of sulphurous and nitrous acid gas, was visibly affected in thirty seconds, and apparently completely asphyxiated in two minutes ; but on being removed immediately to the open air, it was completely recovered in from twenty-five to thirty minutes. But an individual of the same species, when confined in chlorine, was powerfully affected in less than twenty seconds, and became completely motionless in two minutes ; and although it was immediately removed to the open air, it hardly gave any signs of life for more than twelve hours afterwards, and even then it did not ultimately recover. We have thus a distinct proof of the poisonous nature of these gaseous bodies, and of their comparative virulence, and that the respiration of insects is affected by them in precisely the same manner as the respiration of vertebrated animals, the only apparent difference appearing to arise from a peculiar habit of body which resists their effects for a longer or shorter period. But the most deadly of all media is hydrocyanic acid in a state of vapour, admixed with atmospheric air. If an insect be confined over the fumes of hydrocyanic acid, it perishes almost instantaneously if the gas be powerful, but if only a small quantity be mixed with atmospheric air, the insect is paralysed for a time, but will ultimately recover. This difference between the effects of hydrocyanic acid gas and chlorine is very interesting. The instantaneous manner in which hydrocyanic acid gas, or rather cyanogen, destroys life and suppresses every act of respiration and volition, when respired by the insect, sufficiently proves that it cannot be by its admission into the circulation of the body, and that its being received into the system of tracheal tubes is sufficient to enable it to act upon the nervous system instantaneously. Even those insects which in every other medium are exceedingly tenacious of life, even in the deadliest, chlorine, perish in an instant in cyanogen. The insect dies in a tetanic state of contraction of all the muscles of the body. Chlorine, on the contrary, appears to kill by producing in the first place a rigid spasm of the respiratory organs, and a congested state of the mucous membrane, which renders respiration at first difficult and at length impossible.

From these circumstances I have been led to conclude that the manner in which the respiration of insects is affected by noxious media is the same as in Vertebrata, and that life is destroyed by them in precisely the same manner in both divisions of the great kingdom of animated nature.



Having thus considered the means which are employed in the function of respiration in insects, the manner in which it is performed, the quantity of respiration under different circumstances, and its duration in different media, it remains only to notice the relation which these bear to the volume of the structures concerned in the different states and species.

We have seen that in the larva state the respiratory organs in most species are very small, and that it is only in the perfect condition that they acquire the maximum of development. But in the pupa, or intermediate state, these organs are much larger than in the larva, yet the insect requires a much smaller quantity of air for its support in a given time. Hence it follows that although the organs concerned are of greater volume, the activity of respiration is diminished; so that the pupa is enabled to endure the effects of noxious media, or the privation of air, much longer than the larva, and the larva, as in the case of many Hymenopterous insects, longer than the perfect individual. The larva of an insect is analogous to the child, or new-born offspring of the mammiferous animal, and the analogy is the most perfect in its earlier condition. The pupa state bears a relation to the whole life of the insect similar to that which the hybernating condition bears to the life of the hybernating animal. In that state the volume and velocity of the circulation are diminished; the temperature of the body (which I hope to have the honour hereafter of proving to the Society is always higher than the surrounding medium in insects in a state of activity,) is then scarcely, if at all, above that of the atmosphere, and the respiration, as we have seen, is almost entirely suspended. This is exactly the condition of the hybernating Mammalia. When the insect awakes from its pupa state through the influence of external stimuli, its respiration, circulation, and temperature are all increased, and its capability of supporting existence in noxious media is diminished. It is gradually developed into the perfect animal, takes on itself the active duties of its existence, continues its kind, and dies. But even during this its perfect condition it occasionally passes into the hybernating state, which I shall consider more particularly on a future occasion.

*Description of the PLATES.*

PLATE XXXVI.

Fig. 1. Part of a tracheal vessel of the larva of *Papilio brassicæ*, LINN., exhibiting the spiral fibre (*a*) and the external or serous membrane (*b*).

2. The respiratory organs contained within the abdomen of *Bombus terrestris* (Humble-Bee, magnified 10 diameters).

(*a*) Two large brown tracheæ, which pass through the petiole which connects the abdomen with the trunk, and are dilated in the first segment

into the large vesicles (*f*): (*b*) small transverse connecting tube, which gives off a pair of small tracheæ, which, with two others from the large tracheæ, are developed into a very large, superior, transverse vesicle, which lies above the lateral ones in the abdomen: (*d*, *e*) two longitudinally directed tracheæ, which pass on each side of the œsophagus; (*e*) passes down to the lower part of the proventriculus, and distributes recurrent branches, (*d*) passes no lower than the anterior part of the proventriculus: (*g*) funnel-shaped transverse tracheæ, which pass beneath the muscles in the under surface of the body: (*i*, *k*) origins of similar vessels, which pass over the dorsal surface of the abdomen (*h*): (*i*) trachea to the duodenum or ventriculus, (*k*) to the small intestines, (*l*) to the colon and organs of generation.

Fig. 3. A portion of the colon and cæcum from the perfect insect *Phalæna vinula*, LINN., laid open to show the ramifications of the tracheæ in the adipose membrane (*a*), and that they do not ramify in the internal glandular or mucous membrane, a part of which is reflected separately (*b*). Magnified 10 diameters.

4. A portion of the mucous lining of the colon, studded with glands, and separated from the other structures. Magnified 24 diameters.
5. One of the antennæ of *Papilio urticæ*, LINN. removed from the insect immediately after changing to the pupa state, and viewed by transmitted light, and very highly magnified to show the beautiful distribution of the tracheal vessel.
6. The exterior spiracle with its converging fibres. Magnified 25 diameters.
7. The internal spiracle, with its valves, muscles, and nerves. Magnified 25 diameters. (*a*) part of the torn trachea; (*b*) the posterior valve; (*c*) the retractor valvulæ; (*d*) the circular sphincter muscle; (*e*) the retractor spiraculi.

#### PLATE XXXVII.

Represents the muscles, tracheæ, and nervous system of the posterior part of the body contained in the eighth, ninth, tenth, and eleven segments, magnified.

- a. One half of the visceral surface of the eighth segment, with the muscles, nervous cords, and tracheæ *in situ*.
- b. The visceral surface of the ninth segment, with the recti muscles of the right side of the body removed, and the recti and first and second oblique on the left.
- c. The ventral surface of the tenth segment, with the larger and smaller recti and the four oblique muscles removed to show the transverse and spiracular muscles, and the third rectus.
- d. The eleventh segment, containing the double ganglion and termination of the nervous columns.



*Muscles.*

Fig. 1. 1. The great dorsal and ventral recti.

2. The smaller rectus.
  3. The middle line of insertion for the attachment of the greater recti and three oblique.
  4. The posterior or third line of insertion for the smaller recti and third oblique.
  5. The retractor of the stomach.
  6. The first oblique.
  - 7, 8. The second oblique.
  - 9, 10. The third oblique.
  11. The fourth oblique.
  12. The third rectus.
  13. The fifth oblique.
  - 14, 16. The triangularis muscle.
  15. The transverse median muscles.
  17. The transverse abdominal muscles.
  18. The anterior abdominal.
  - 19, 20. The lateral abdominal.
  21. The sixth or posterior oblique.
  22. The seventh or postero-lateral oblique.
  23. The first transverse lateral muscle.
  24. The second transverse lateral muscle.
  - 25, 26. The retractor of the spiracle.
  27. The retractor of the valve of the spiracle.
- e. The longitudinal trachea of the right side, with its ramifications.  
 f. A portion of the trachea cut away to show the entrance of the spiracle.  
 g. The spiracle with the nerves and muscles belonging to it.

*Nerves.*

- H, I, K. The nervous column of the segments, exhibiting the ganglia of the sensitive tract traversed longitudinally by the motor tracts of the cords which terminate upon the last or double caudal ganglion, by dividing each into two portions, one of which is given to each of the four terminal nerves. It exhibits also the transverse nerves, forming a triangular plexus above the cords anterior to each ganglion, and passing laterally on each side to distribute their branches on the visceral surface of the muscles.
- a. The ganglion and transverse nerves.
  - b. The transverse plexus.

- c.* The first branch of the transverse nerves, passing over the ganglion, and converging behind it, to form the longitudinal tract (*d*).
- e.* The second branch.
- f.* The first or great moto-sensitive nerve.
- g.* The third branch of the transverse nerve.
- h.* Its looping over the second rectus, to unite with the moto-sensitive.
- i.* The third branch and its plexus.
- k.* Its union with another moto-sensitive nerve.
- j.* Portions of this nerve given to the insertion of the recti muscles.
- l.* The fourth branch of this nerve.
- m.* The trunk of the transverse nerve divided behind a tuft of tracheæ.
- n.* Union with the great moto-sensitive nerve.
- o.* Distribution of transverse nerves to the lateral oblique and rectus muscles.
- p.* First branch of the great moto-sensitive nerve (*f*).
- q.* Second branch of this nerve.
- r.* Third branch.
- s.* Fourth branch.
- t.* Division of the nerve into two branches.
- u.* A plexus, formed by the interweaving of the branches.
- v.* Branch given to the first, second, third, and fourth oblique and great rectus.
- w.* Union of the nerve with one of the transverse nerves.
- x.* Course of the nerve to be distributed to the latero-abdominal muscles.
- y.* Branches to the abdominal muscles.
- z.* To the transverse and latero-abdominal muscles.
- 32. The third branch of the second division of the first or great moto-sensitive nerve, giving ramifications to the muscles 17, 18, 23, 24.
- 33. The second or oblique moto-sensitive nerve.